THE PHOSPHORESCENCE OF RENILLA.

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The phosphorescence of the sea-pansy *Renilla* has been known for a long time. As early as 1850 Louis Agassiz observed that *Renilla reniformis,* the common species of our southern waters, "shines at night with a golden green light of a most wonderful softness." This is also true of *Renilla amethystina* of southern California. If a fresh specimen of this species that has been exposed to daylight is carried into a dark-room and stimulated by being gently prodded, no phosphorescence is observable, but if the same experiment is tried at night, the colony glows with a wonderfully clear blue-green light.

If during daylight non-phosphorescent Renillas are transferred to a dark-room and kept there, they begin to show phosphorescence on stimulation in about half an hour and attain what seems to be their maximum under these circumstances in about an hour. The phosphorescence thus developed seems never to reach the degree of brightness seen during the night. This probably depends upon a natural daily rhythm in the animal's metabolism. Phosphorescence induced during the daytime by placing a colony for an hour or so in the dark is completely lost on exposure to daylight for about five minutes. If during the night a colony that showed a naturally acquired bright phosphorescence is illuminated by strong light, the ability to produce light steadily decreases, but is never entirely lost, showing that either artificial light is not so effective in this respect as daylight or that during the night *Renilla* is more efficient in producing the substances necessary for the production of light than during the day.

Renilla is phosphorescent only on stimulation. If in the night a spot on its upper surface is stimulated mechanically or electrically, luminous ripples emanated from this spot and spread out concen-

trically over its surface like waves on the smooth face of a pond into which a pebble has been thrown. If a fine needle point is used as a stimulus, a single point of light can be excited and this point will glow some seconds but without becoming a center from which luminous waves spread.

When a glowing *Renilla* is examined under a hand lens, the parts from which the light emanates are seen to be small masses of light-colored material that stud the upper surface of the animal and that surround the bases of the zooids. Apparently light emanates from no other source. No phosphorescence has ever been excited from the peduncle by which the animal anchors itself in the sand, nor from the under surface of the disc. The phosphorescence is strictly limited to the upper surface and apparently to the light-colored material of that surface. If a bit of this material is cut from the disc at night-time and carried into a dark room and crushed between glass, a momentary sparkling can be seen. If this experiment is tried with a bit of the purple flesh of the upper surface, no such sparkling is produced. Hence it is clear that the source of the phosphorescence is the light-colored material of the upper surface of the disc.

This light-colored material on close inspection is seen to be composed of two substances: a whitish chalky substance and a light-yellowish crystalline one. These two substances are so intimately associated that it is impossible to separate them satisfactorily or in most places to determine by direct inspection which is responsible for the light. Only on the edge of the disc is it possible to make decisive observations. Here the two substances form a well-marked double fringe, the outer one being composed exclusively of the white material, the inner one of the yellowish. When phosphorescence is excited on the adge of the disc, it can be seen that the light is resident in the white fringe and not in the yellow and hence the former material must be regarded as the true source of the phosphorescence. When this material in a luminous state is inspected under a hand lens it is indescribably beautiful; the light it gives out is of an intense blue-green color with all the play that one sees in a brightly illuminated opal.

The mechanical or electrical stimulation of *Renilla* at night re-

sults in what seems to be a series of luminous waves that emanate concentrically from the region of stimulation. When one of these wave fronts is closely scrutinized, it is found to be not a continuous line but a series of luminous points which represent the small masses of white material already alluded to and which for the moment lie in what would be a continuous wave front. Thus the appearance of a luminous wave is due to the momentary glowing of one concentric line of points after another as the impulse that induces the phosphorescence spreads from the center of stimulation outward.

When the disc of *Renilla* is cut into and the animal is subsequently excited to phosphoresce, the luminous waves pass round the incisions without interruption so long as organic continuity is present. If the disc is cut nearly in two transversely, the waves of phosphorescence can be started in either piece and will pass thence over the connecting bridge to the other place. If the disc is cut into a scroll that can be unfolded into an elongated form, stimulation at one end will start a luminous wave that will pass to the other.

If a *Renilla* is split longitudinally through its chief axis, the two halves remaining attached only through the distal part of the peduncle, the stimulation of one half calls forth a flash of light in that half which, after it has subsided, is followed by another flash in the other half. The second flash follows the first at such an appreciable interval of time that the preparation seems to wink first with one eye and then with the other. Here the interval between flashes is due to the transmission of the wave of excitation through the non-luminous peduncle, for if the peduncle is completely split no such transmission occurs even if the two halves are closely applied to each other. This observation shows that the luminous waves are under the control of some form of transmission, non-luminous in character, that spreads in wave-like fashion and for which the phosphorescent waves may be said to be luminous replicas. It also makes clear that the peduncle can transmit the impulses that excite luminosity in other parts. Not only can be peduncle transmit these impulses, but it can also originate them, for if the tip of the peduncle of *Renilla* is pinched, after a moment the disc flashes in waves of phosphorescence.

As might be inferred, any portion of the disc carrying the white

material already alluded to can on stimulation be made to glow. Thus right or left halves, quadrants, centers, margins or even minute fragment will on appropriate treatment give out light.

The impulses that induce phosphorescence are profoundly influenced by such anesthetics as magnesium sulphate. If a preparation is made by cutting a disc of *Renilla* almost in two by a transverse incision and, after determining that the connecting bridge will transmit luminous waves, this bridge is covered with crystals of magnesium sulphate, the waves of light in ten minutes or so will be blocked at the bridge and light will be produced in only that part of the disc which is directly stimulated. After half an hour or so in pure seawater the bridge will again transmit the luminous waves.

If a V-shaped preparation is made from a *Renilla* by splitting it through its long axis except at the distal end of the peduncle, it will be found, as already stated, to transmit impulses for light production from one half to the other through the partly split peduncle. If the unsplit portion of the peduncle is now covered with crystals of magnesium sulphate, in five to ten minutes no impulses to illumination will pass through it, for when one half is excited to glow the other does not follow by producing a flash. Recovery from this condition occurs after the preparation has been for half an hour or so in pure seawater.

The rate at which the luminous waves traverse the disc of *Renilla* is a relatively slow one. To determine, it, strips of tissues were cut from the edge of the disc and pinned out in seawater. They measured five to eight millimeters in width and about ten centimeters in length. After night had come on these strips could be stimulated by touching one end gently with a metal rod whereupon a single wave of light would pass rapidly over the length of the strip. This could be timed by a stop-watch. Five such preparations were tested with the result that the average rate of transmission was found to be 7.39 centimeters per second. This rate agrees almost exactly with that for the withdrawal of the zooids in Renilla, namely 7.83 centimeters per second and indicates that both these processes are controlled by a single mechanism. As these rates are close to that of the nerve-net of the sea-anemone *Metridium,* namely, 12 to 14 centimeters per second, the common mechanism upon which

they depend is probably nervous. Certainly these rates are in strong contrast with the rates of transmission of certain peristaltic movements that are known to pass over the peduncle and the disc of *Renilla*. These travel 0.15 centimeters to 0.12 centimeters per second, one fiftieth to one sixtieth as fast as the other waves do, and are very probably muscular in origin. Hence, the conclusions that the withdrawal of zooids and the phosphorescence of *Renilla* are controlled by a single form of transmission and that this transmission is neurogenic rather than myogenic in origin.

If the transmission by which the phosphorescent waves of *Renilla* are produced is nervous in character, it ought to vary with the temperature and such seems to be the case. Thus in one set of trials the rate per second was found to be at 11° C. 4.0 centimeters, at 21° C. 7.7 centimeters and at 31° C. 20.7 centimeters. In another set it was at 15° C. 6.5 centimeters per second, at 20° C. 8.3 centimeters and at 25° C. 12.2 centimeters. As is shown in the second set, an increase of 10 degrees in temperature is accompanied by an approximate doubling of the rate, 6.5 to 12.2 centimeters per second. Much the same is true of the first set except for its highest member. If in this set the rate per second at 21° is taken to be 7.7 centimeters, at 11° it ought to be half that or 3.85 centimeters which is very close to the oserved rate of 4.0 centimeters per second. On the same basis at 31° a rate of twice 7.7 centimeters or 15.4 centimeters per second should be looked for but the rate actually observed was somewhat higher than this, namely 20.7 centimeters per second. Notwithstanding this divergence, which is associated with a rather extreme temperature, it may be stated that over the greater part of the temperature range for every interval of 10 degrees the higher rate is approximately twice the lower one. Although the usual interpretation of this condition has been more or less questioned recently, it is generally assumed, in accordance with the van't Hoff law, that such relations in rates are indicative of chemical rather than of physical processes, an assumption that would aline the kind of transmission that occurs in the phosphorescent wave of *Renilla* with the burning of a trail of gunpowder rather than with some form of transmission of a purely physical type.